7. The zooplankton

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The zooplankton community includes about 30 species or genera of Rotifers (Pourriot 1968; Robinson 1971) and several microcrustacea. During the high water period, the latter were represented mainly by 8 species of Cladocera (*Diaphanosoma excisum*, *Daphnia barbata*, *D. longispina*, *D. lumholtzi*, *Ceriodaphnia cornuta*, *C. affinis*, *Moina micrura dubia*, *Bosmina longirostris*), two Calanoids (*Tropodiaptomus incognitus*, *Thermodiaptomus galebi*) and three *Cyclopoids (Thermocyclops neglectus*, *Th. incisus circusi*, *Mesocyclops* cf. *leuckarti*). A Cyclopoid (*Thermocyclops tchadensis*) and two unidentified Calanoids of secondary importance can be added to the list. The littoral forms of the Cladocera and Copepods, mostly attached to the vegetation were much more numerous (Dussart and Gras 1966; Rey and Saint-Jean 1968, and 1969).

During the period of 'Normal Chad', the planktonic and littoral faunas were clearly separate. However, two exceptions were noted: *M. leuckarti*, normally found in grassbanks, and a species of *Alona* with a particular affinity for the center of grassbanks were also found in the open water in 1970–71. *Alona* became frequent in plankton samples during the period of 'Lesser Chad'. This species is very abundant in the open areas within grassbanks, in contrast to other littoral species which are actually attached to the vegetation (Dejoux and Saint-Jean 1972). This location causes this chydorid to be swept from the grassbanks by water currents and during storms and this could explain its incidental presence in the plankton.

Most of the species recorded up to the present from different parts of the lake are fairly widespread in Africa, or more generally in the intertropical regions. There were three cosmopolitan species among the planktonic forms: *B. longirostris*, *D. longispina*, and *M.* cf. *leuckarti*. The importance of the biomass of the two Cladocerans above, as well as the diversification of the genus Daphnia (3 species) must be emphasized.

The data collected on the zooplankton cover a period of lake recession, from 1964 (high waters) to 1975 ('Lesser Chad'). They are distributed very heterogeneously in space and time and are of three types: the annual cycles at one or several stations (1964–65, 1972 to 1975); observations covering a large part of

J.-P. Carmouze et al. (eds.) Lake Chad

ISBN 90 6193 106 1. Printed in the Netherlands

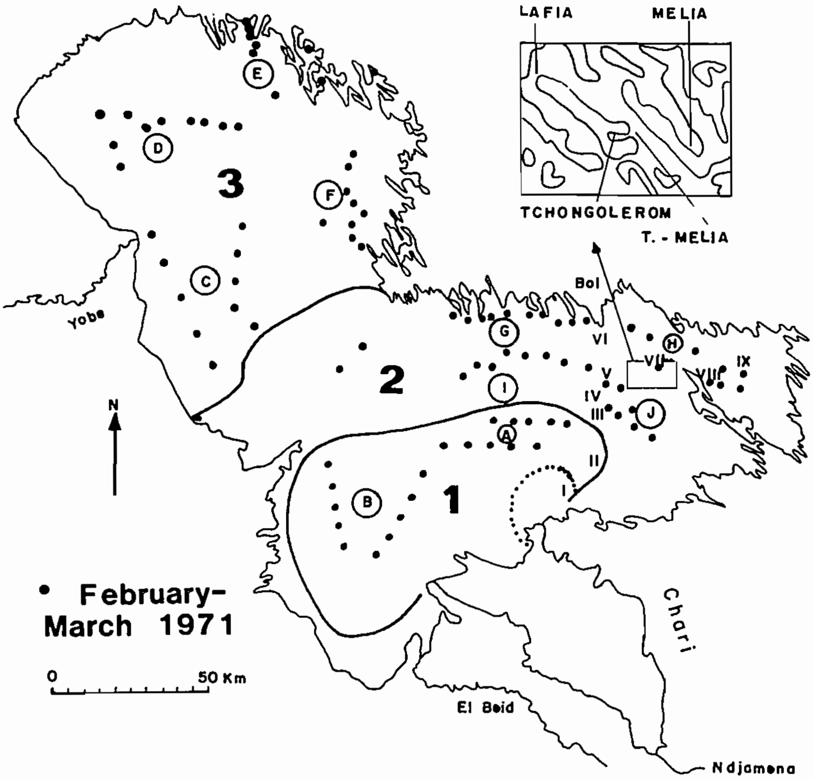

Fig. 1 The major ecological zones and stations sampled during the period of 'Normal Chad'. The Roman numerals designate the stations sampled over the course of the annual cycle of 1964–65; the dots and the letters correspond to the survey of February 1971; the stations sampled from 1968 to 1973 are framed.

the lake and collected at a given time of the year (February 1971); observations much more restricted in space and time (one station visited occasionally) (Fig. 1). We also have some information collected during 1967–68 by Robinson and Robinson (1971) on the annual cycle for the whole of the north basin.

All samples except those of Robinson and Robinson were taken by vertical tows from the bottom to the surface using one or two truncated nets of 1.5 m length, 30 cm opening diameter, and 60 µm mesh size. Robinson used oblique tows with a net of 60 or 200 µm mesh size and 30.5 cm diameter opening. The counts were made on subsamples taken with a calibrated syringe, representing 1 to 10% of the sample according to the abundance of the organisms. The individual weights by species or stage were used for biomass calculations and are shown in Table 1 as well as in Table 6 of Chapter 12.

7.1 The zooplankton of 'Normal Chad' (1964–71)

This period was characterized by a continuous mass of water, with a community that was relatively uniform in composition and structure. Excluding the Rotifer *Brachionus plicatilis*, which is well known in water of high salinity (Pourriot et al. 1967), and was only present in the regions of high conductivity at the extreme north of the lake, no variations appeared in the species composition in relation to water salinity. Nearly all the species recorded were present in the different regions sampled. Although very diverse the community was dominated by Calanoids, which represented about 46% of the biomass during 1964–65 in the eastern archipelago of the southern basin (37 and 17% for the Cladocera and Cyclopoids). There were, however, some regional and seasonal variations in biomass that appeared to be related to the hydrology of the Shari, or to other factors.

The Rotifers represented a negligible part of the biomass, particularly during the period of high waters, and will not be considered here.

7.1.1 *Regional and seasonal variations in abundance: the major ecological zones of the lake*

From the data of 1964–65 (Gras et al. 1967) and February 1971 (Carmouze et al. 1972) the lake can be divided into three zones defined in Fig. 1, differentiated on the basis of the frequency distributions of biomass observed in the February 1971 survey (Fig. 2).

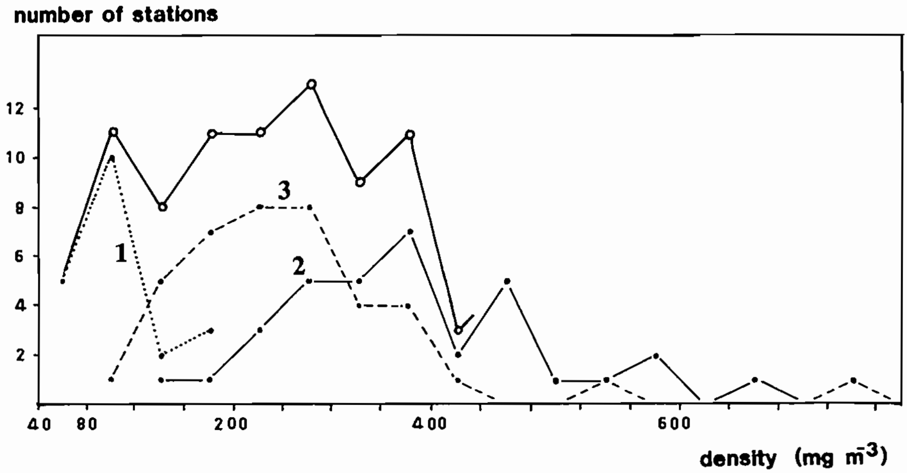

Fig. 2 Frequency distribution of biomass in samples taken in February 1971 in the north basin (zone 3, – – – –), the archipelago of the south basin (zone 2, ———), and the open waters of the south basin (zone 1, ...); total of 3 zones: O——O.

7.1.1.1 *The open water of the southern basin (zone 1).* The open water was characterized by low densities for a long period, approximately June to February, and by a strong but brief increase during April (Fig. 3b, station II). During 1964–65 the average biomass between June and February was thus about 120 mg m^{-3} (96 individuals per liter), and the ratio between the annual maximum and minimum was 6.3 (biomass) and 10.3 (numbers). The values in 1971 (average 93 mg m^{-3} for 20 stations covering the whole zone) and from October–November 1969 (35 mg m^{-3}), confirm the low density that characterized this zone for most of the year. In the regions close to the delta represented by station I during 1964–65 (Fig. 3a), and sampled again during the flood of 1969, the minima were almost zero during October–November. These regions formed a 'perideltaic zone' which can be included in zone 1.

The comparison of the numbers of copepodites and adults of Cyclopoids and Calanoids, in stations O, I and II during April 1965 (maximum abundance) showed the differentiation of a river and deltaïc plankton (station 0) dominated by Cyclopoids, from plankton of stations I and II where the Calanoids were abundant. The ratio Cyclopoids/Calanoids was almost 10 at station 0, 0.7 at station I and 1.2 at station II. It was 1.2 in the reed islands and the archipelago (stations III to IX) during April 1965, with an annual average of 2. This difference suggests that the development of lake plankton in the peri-deltaïc region was independent of river inflows. These supplies were moreover very low at the time of the planktonic explosion observed in the region at the beginning of the year (Fig. 3a, station I).

7.1.1.2 *The archipelago and the reed islands of the southern basin (zone 2).* The biomasses here were clearly much higher than those in zone 1, and the annual variations were low. In the archipelago the annual average in 1964–65 (station V to IX) was 333 mg m^{-3} (318 ind. l^{-1}) and the maximum/minimum ratio was 2.2 (biomass) and 2.0 (numbers). Two minima were seen, one corresponding to the low water of the lake and the rainy season (June–September) and the other to the cold season (December–March), as well as two maxima, during April–May and during October–November. The few complementary data reported in Fig. 3 confirmed the higher level of biomass in this region of the lake. The archipelago region also appeared to differ from zone 1 in having a greater abundance of the genus *Daphnia*. An average of one individual per liter was found in station I and II compared with an average of 10 individuals in stations V to IX, which corresponded to the density of the genera *Moina* and *Diaphanosoma*, whose distribution in the lake was more uniform. The average density of *Daphnia* in the reed island region (stations III and IV) was intermediate: 3 l^{-1}.

The transitory character of the reed islands (Chap. 2) was reflected at the level of community composition and abundance as shown above for the genus *Daphnia*. So, in 1971 (Table 1), some biomasses were much higher in the reed

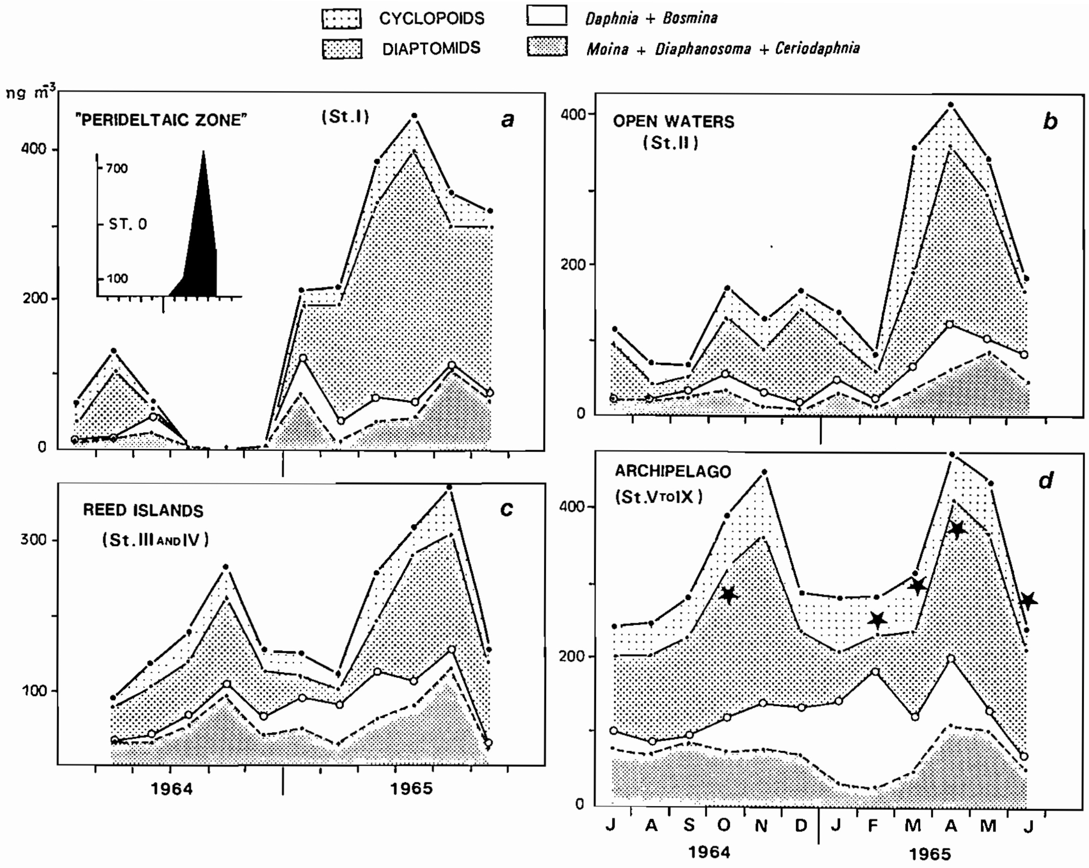

Fig. 3 Annual variations of principal group cumulative densities 1964–65 in the peri-deltaic and deltaic regions (a); in the open waters (b); in the reed islands (c); and in the archipelago (d) of the south basin; * other data.

Table 1 Density in mg dry weight m^{-3} and in number of individuals l^{-1} in different regions of the lake during February 1971 (14/02/71 to 4/03/71). N, C, A, E: Nauplii, Copepodites, Adults, Eggs. The letters A to K refer to Fig. 1. The specific weight (µg) given in brackets have provided the biomass.

Species	Regions										
	Zone 1		Zone 2					Zone 3			
	Series		Series					Series			
	A	B	G	H	I	J	K	C	D	E	F
The *Diaphanosoma* (2.5 µg)	9.0	5.0	20.0	17.5	75.0	68.8	31.5	8.0	0.3	0.8	6.8
Moina (2.3)	12.0	3.7	20.0	3.2	49.0	47.2	24.4	6.4	1.8	0.5	3.9
Ceriodaphnia (1.0)	0.7	0.1	0	0	7.7	19.9	0	0	0	4.0	0
Daphnia (3.0)	6.0	1.5	20.7	0.6	21.6	16.8	137.4	13.8	74.1	59.1	71.1
Bosmina (0.75)	5.6	3.7	58.0	104.9	51.2	21.5	73.0	46.3	24.8	17.6	62.6
N. Cyclopoids (0.05)	3.5	3.8	6.9	8.0	11.0	7.9	5.3	4.9	4.5	5.3	4.4
C. Cyclopoids (0.55)	16.6	8.4	13.7	24.6	29.5	26.3	23.2	16.4	22.1	21.8	17.4
A. *Th. neglectus* (2.15)	4.9	11.6	19.6	34.2	37.6	19.1	21.3	10.3	9.5	11.4	9.2
A. *Th. incisus* (3.5)	1.1	0.7	4.9	4.6	3.2	1.8	6.3	3.2	4.2	0.7	4.6
A. *Mesocyclops* (5.0)	1.0	3.0	2.5	5.0	2.5	0.5	9.0	11.0	7.5	9.5	4.5
N. *Tropodiaptomus* (0.4)	1.4	0.7	3.2	5.1	2.9	1.5	4.5	1.0	0.9	3.5	1.4
C. *Tropodiaptomus* (3.8)	16.7	25.8	15.6	17.5	27.4	37.2	17.9	22.4	9.1	41.4	6.8
A. *Tropodisptomus* (11.0)	14.2	24.2	48.4	47.3	45.1	55.0	40.7	45.1	30.8	90.2	20.9
E. Cyclopoids (1.5% A. biom.)	0.1	0.2	0.4	0.7	0.6	0.3	0.5	0.4	0.3	0.3	0.3
E. Calanoids (1.5% A. biom.)	0.2	0.4	0.8	0.7	0.7	0.9	0.6	0.7	0.5	1.4	0.3
Cladocera											
weights	33.3	14.0	118.7	126.2	204.5	174.2	266.3	74.5	101.0	82.0	144.4
numbers	19.0	9.1	100.9	148.5	134.5	102.2	166.3	72.3	58.6	47.6	111.5

Cyclopoids											
weights	27.2	27.7	48.0	77.1	84.4	55.9	65.6	46.2	48.1	49.0	40.4
numbers	103.2	97.4	174.6	223.4	292.0	215.8	161.9	136.0	136.4	152.5	126.4
Calanoids											
weights	32.6	51.1	68.0	70.6	76.1	74.6	63.7	69.2	41.3	136.5	29.4
numbers	9.1	10.7	16.5	21.6	18.5	18.5	19.6	12.6	7.5	27.9	7.2
Total											
weights	93.1	92.8	234.7	273.9	365.0	304.7	395.6	189.9	190.4	267.5	214.2
numbers	131.3	117.3	292.0	393.5	445.0	336.5	347.8	220.9	202.5	228.0	245.1

islands (series I and J) than in the actual archipelago (series G and H, Fig. 1), and the opposite was seen during 1964–65, when the average biomass of stations III and IV (190 mg m^{-3}) was clearly lower than that of the archipelago, and in the same range as that of the open water (180 mg m^{-3}). Seasonal variations were identical in the two regions. This last fact shows a decrease in the influence of the hydrological regime of the Shari, linking the reed islands to the archipelago. The two form an heterogeneous complex from the point of view of densities, and this is clearly shown in the frequency histogram of biomasses (Fig. 2, zone 2).

Seasonal variations mainly affected the Cladocera and Calanoids. In the first, the genera *Bosmina* and *Daphnia* were dominant during the cold season, and the genera *Moîna*, *Diaphanosoma* and *Ceriodaphnia* were dominant for the rest of the year. As a whole, the Cladocera had their lowest density between June and September (less than 100 mg m^{-3} or 63 ind. l^{-1} on average), and the highest densities between October and May (114 to 199 mg m^{-3}, 102 ind. l^{-1}). The Calanoids were less abundant during the cold season (84 and 61 mg m^{-3} during January and February, 9 ind. l^{-1} on average without the nauplii), and showed two very high maxima, during October–November (220 and 224 mg m^{-3}, 34 ind. l^{-1}) and during April–May (238 and 273 mg m^{-3}, 35 ind. l^{-1}). This group was therefore responsible for most of the annual variation in zooplankton abundance.

The Cyclopoids as a whole only showed irregular small-scale variations. However, the *Mesocyclops* adults were less abundant during the cold season than during the warm season, and the *Thermocyclops* adults behaved in the opposite way (Fig. 4).

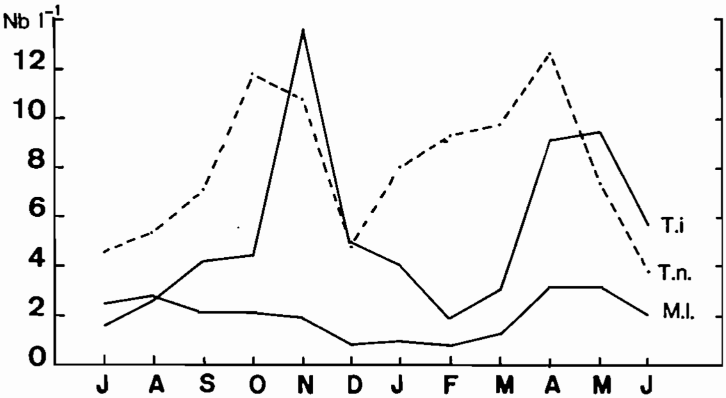

Fig. 4 Annual variations in the number of adults (Nb l^{-1}) of *Tropodiaptomus incognitus* (T.i) of *Thermocyclops neglectus* (T.n.) and *Mesocyclops leuckarti* (M.l.) in 1964–65 in the southern archipelago.

The winter plankton of the southern Archipelago (December to March), contained relatively few Calanoids (32% of the biomass) and more Cladocera (49%), two thirds of them belonging to the genera *Daphnia* and *Bosmina*. The corresponding annual averages were 46% for the Calanoids and 37% for the Cladocera, of which 46% *Daphnia* and *Bosmina*.

The preceding seasonal variations were confirmed by the winter nature of the community in February 1971 (Table 1), which contained 27% Calanoids, and 48% Cladocera (75% *Daphnia* and *Bosmina*), in the actual archipelago (series G and H). Similar variations were also observed in the reed islands. Finally, a similar development of the Calanoids was observed in the open water (station II), with a marked increase during April–May and a smaller increase during October–November, which may have been limited by the arrival of the Shari flood waters. It is necessary, however, to point out that the April 1968 population at Melia (Table 2) did not conform to the seasonal model, since among the Cladocera, the genera *Daphnia* and *Bosmina* were dominant, forming 75% of this group. This anomaly could be explained by the observed temperatures being lower than in 1965: 28°C during April 1965 and 24.5°C on average during April 1968.

7.1.1.3 *The northern basin (zone 3)*. Only the data of February 1971 allows a strict comparison of the zooplankton populations from the northern and southern regions of the lake. Based on these data, the northern basin was relatively homogeneous in density (Fig. 2 and Table 1). The average density (215 mg m^{-3}) was significantly lower than in the southern archipelago (254 mg m^{-3} for the series G and H) and of course in the entire zone 2 (315 mg m^{-3} for the series G to K). Except for the dominance of the genera *Daphnia* and *Bosmina* during the cold season, the observations by Robinson and Robinson (1971) for one annual cycle during 1967–68, showed that there was no seasonal variation in community abundance as in zone 2. Any such variation would not affect the Calanoids, but the observations of February 1971 were contradictory in this respect. The zooplankton then contained the winter population seen in zone 2, with 32% Calanoids and 47% Cladocera (92% *Daphnia* and *Bosmina*).

The densities observed by Robinson and Robinson, especially in April 1968, were 3 or 4 times lower (if considering numbers and biomass), than the values observed in the archipelago of the southern basin, the only region of this basin which could have been compared with the north*. Such a difference can only be explained by admitting that the sampling techniques used in the north (oblique tows of a small size net) caused net-avoidance and so underestimate zooplankton abundance.

The observations from 1967–68 thus confirmed the low level of density in the

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* A misinterpretation of Robinson's data has led to a much higher annual biomass for the northern basin in an earlier work (Carmouze et al., 1972).

Table 2 Changes in zooplankton abundance (mg d.w. m^{-3}) between 1964 and 1975 in various stations of the archipelago of the south basin (cf. Fig. 1 and Table 1). 1971: mean of series G and H; 1968: estimated density of Cyclopoid (italics); 1972 and 1973: means of Tchongolerom and Tchongolerom-Melia stations (except May and August 1973); in 1972, the values in italics are the means of May and June series, and the others of 5 series sampled in May, July, August and October. N, C, A designate respectively the nauplii, the copepodites and the adults; NE not evaluated.

	1964–65	1968	1971	1972	1973				1974–75
	South Basin	Mélia	Ser. G and H	Tchong. + T-Mélia	Janu.	March	May	August	Bol
					Tchong. + T-Mélia		Lafia	Bol	
Daphnia	27.8	9.7	10.7	0.9	0	0	0	0	0
Ceriodaphnia	23.1	0	0	2.8	0	0.3	0	0	0.2
Moina	16.5	22.8	11.6	19.7	18.6	24.1	28.3	0.1	12.9
Diaphanosoma	27.5	18.6	18.8	28.0	3.9	6.7	29.0	0.1	10.9
Bosmina	29.6	90.0	81.5	*1.9*	3.5	0	0	0	0
N. Cyclopoids	7.5	8.2	7.5	*6.2*	5.4	29.6	58.2	N.E.	N.E.
C. Cyclopoids	22.4	16.3	19.2	*14.2*	21.4	43.4	31.4	0.5	11.1
A. *Th. neglectus*	14.5	24.5	26.9	10.8	42.5	124.3	81.7	3.1	21.0
A. *Th. incisus*	10.5	8.9	3.8	6.1	1.5	11.0	12.6	ε	0.2
A. *M. leuckarti*	1.5	7.3	4.8	1.6	1.6	ε	0	0	0
N. Calanoids	3.1	15.7	4.2	*3.7*	0.5	1.9	1.0	0	0
C. Calanoids	62.9	51.7	16.6	*24.3*	7.3	9.2	1.2	0	0
A. *Tropodiaptomus*	70.5	113.8	48.6	51.4	12.1	ε	0	0	0
A. *Thermodiaptomus*	15.4	4.3	ε	57.4	87.5	74.0	36.3	0	0
Cladocera	124.5	141.2	122.5	*71.9*	26.1	30.9	57.3	0.2	24.1
Cyclopoids	56.4	65.4	62.6	*45.4*	72.4	208.3	183.9	3.6	32.3
Calanoids	151.9	185.5	69.3	*145.8*	107.5	85.1	38.5	0	0
Total	332.8	392.0	254.4	263.1	205.9	324.3	279.7	3.9	56.4

northern basin. It is probable that the difference between zones 2 and 3 was well represented by the ratio (density in zone 2)/(density in zone 3) observed in February 1971: 1.5 for biomass and 1.6 for individuals.

7.1.2 *Variation factors*

The data presented here show that the densities were relatively homogeneous over the entire lake in April–May. These months corresponded to raised temperatures, lowering of the Shari, an average water level (by comparison to yearly variations) and the period of wind reversal from the harmattan of the NNE to the monsoons of the SSW. In addition to this short period, regional and seasonal variations already described were established, of which the most important occurred in the middle of the southern basin of the lake. Among the primary factors which appeared to regulate these variations were turbidity, the Shari flood, water depth, and the annual thermal gradient. Other factors such as the spatio-temporal variations affecting the zooplanctophagous fish species or the seston doubtless modified them, but the available data did not permit analysis of these probable interferences.

7.1.2.1 *The turbidity of the water.* The open water of the southern basin was differentiated from the rest of the lake mainly by the persistence of very low densities during most of the year. They were about 3 times lower than those of zone 2. The decrease in biomass in zone 1, represented by station II, probably commenced in June with the co-occurrence of a seasonal lowering of lake level and the presence of monsoon winds blowing onto the region at this time of year. They caused a major re-suspension of sediment, rich in mineral particles and increased turbidity, accentuating the decreasing transparency which started in January at this station (Fig. 5). Decrease of the phytoplankton followed after a slight delay so that the zooplankton decrease during June was difficult to explain with the available data, although it was highly likely that the sediment re-suspension was the main factor.

This mechanism persisted until about August–September and the low abundance of zooplankton at this station was thus maintained by the activity of the Shari flood and the lowered winter temperature.

7.1.2.2 *The flood.* In the delta and in the open water, the flood occurred on average from August to December, with a maximum in October–November. The water, muddy at first, was extremely poor in plankton. The massive arrival of this water at first pushed back and then diluted the lake water, resulting in a displacement in time and space of the minimum zooplankton abundance. The results of sampling along several transects starting from the delta during the 1969 maximum flood, give an illustration of this phenomenon (Fig. 6). Such mechanical effect of the floods, frequent in estuarine zones, is particularly

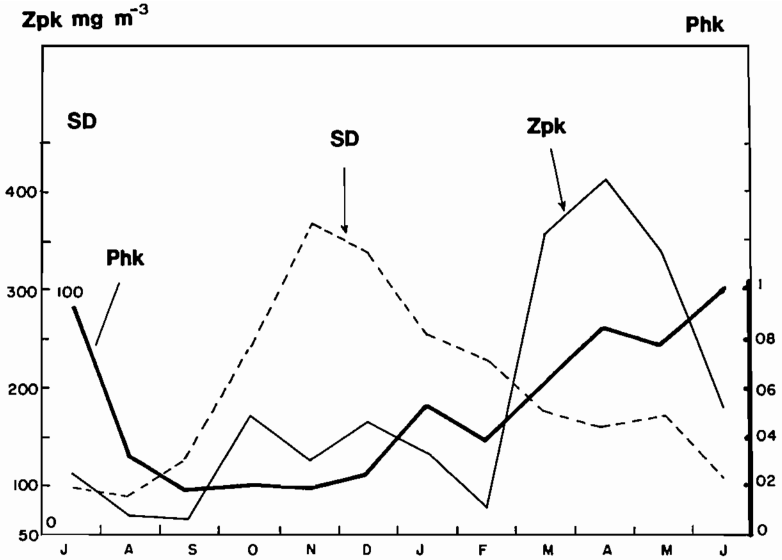

Fig. 5 Variation of Secchi disc transparency (SD, in cm), zooplankton densities (Zpk, in mg m^{-3}) and phytoplankton (Phk) expressed by ratio to a value 1 in June (after Gras et al. 1967) in the southern open waters (st. II) from July 1964 to June 1965.

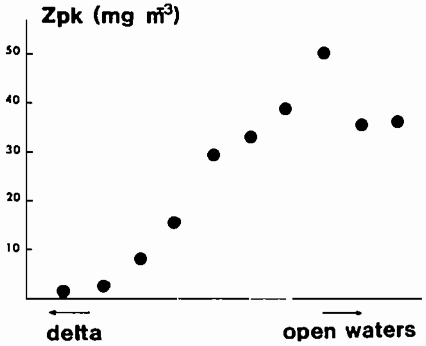

Fig. 6 Variation of density from the delta to the open water during the flood of 1969 (from 11 to 17 November).

comparable with that pointed out by Brandorff and Andrade (1978) for a lake in the Amazonian system. In Lake Chad, it probably had a fairly reduced importance spatially and temporally. As already seen, among the open water and the river system, the flood caused a differentiation of a perideltaïc zone in which the population densities reached zero values (station I, Fig. 3a).

The influence of the flood on the population of station II during October–

November is very problematic. In this station, the minimum densities did not occur during the passage of the flood, but during low water and at the beginning of the flood (June–September). The months of October and November were characterized by increased transparencies (reliable supplies from the Shari floods, increasing lake level, NNE winds) and low algal densities (Fig. 5). The dilution of the environment by the flood waters and low algal densities no doubt limited Calanoids and other zooplankton development. This limitation could have been due to very intense grazing as the ratio between the zooplankton stock and phytoplankton was then higher than at any other time of the year at this station, or throughout the year in the adjacent archipelago.

There was practically no effect of the flood in zone 2 with the maximum abundance occurring in October–November. The algal densities during the winter period, at the maximum lake level, were also relatively high, at least in the actual archipelago. The lesser influence of the Shari in zone 2, allowed the biological factors to be more important conferring to this zone the character of a closed lake.

7.1.2.3 *The depth.* Water depth was one of the most important differences between zones 2 and 3, and one can attempt to relate the lower densities of zooplankton observed in the north, to the increased depth which characterized this zone (about 2 m greater than the south basin). A possible explanation is that, at any one time, a quantitative ratio exists between the primary production of a homogeneous biotope (zone) and its zooplankton standing crop, the former operating in the surface layers whose thickness does not vary in proportion with the depth, so that an increase in depth corresponds to a decrease in the density of zooplankton under a given surface area. The reality is of course not so straight-forward, and the situations encountered are without doubt very diverse. Morever, it is difficult to know if such an explanation is acceptable for a productive shallow lake, which receives significant allochthonous supplies. Be that as it may, the observation of Brandl (1973) and other authors reported by him, tend to support this supposition. In Lake Lipno (6 m average depth), Brandl gives a relationship of the form $d = az^{-b}$ between the average biomass per m^3, observed under 1 m^2 of surface for the whole water column, and the depth z in meters at this site, a and b being two constants ($b \simeq 0.26$). This hypothesis is also supported by the ratio between the phytoplankton (in mg m^{-3} fresh weight) (Iltis 1977) and zooplankton (in mg m^{-3} dry weight) in zones 2 and 3, being respectively 1400/315 (4.4) and 1059/216 (4.9) and thus close. On the other hand, the density found in series I and J in February, 1971 (335 mg m^{-3} for an average depth of 1.60 m) was clearly higher than that of the much deeper series G and H (254 mg m^{-3} for 2.60 m).

The preceding explanation would thus suggest two types of relationship, between the depth of a region and the quantity of plankton present. Below a certain depth threshold and in regions very exposed to wind action, this factor would have a negative effect, analogous to the biomass decrease recorded at station II at low waters. In the most general view, or above the threshold, the densities would tend to increase when the depth decreases. This criterion can be particularly important in shallow lakes.

7.1.2.4 *The temperature*. It is probable that the variations of the Cladocera (dominance) of the genera *Daphnia* and *Bosmina* in winter and the genera *Moina*, *Diaphanosoma* and *Ceriodaphnia* the rest of the year), were related to the strong annual variation in lake water temperature (12°C). Experimental data on development rates (Gras and Saint-Jean 1976b, 1978), suggest that the first two genera are less adapted to increased temperature than the other three. *Daphnia* and *Bosmina* thus have slow development rates, relatively low optimal embryonic development temperatures (22°C for *Daphnia barbata* and 21°C for *Bosmina*) and an optimal zone (the above optimal temperature ±6°C) which does not include temperatures of 28–30°C which existed in the lake during a major part of the year (from April to October in 1964–65). The three other genera, on the contrary, have rapid development rates, high optimal temperatures (24.6 25.3, 23.7°C, respectively) and an optimal zone clearly falling within the range of temperature found in the lake (18–30°C). Moreover, the duration of embryonic development of *Daphnia* and *Bosmina* is lower than that of the three other genera at lower temperatures (<22°C), the situation being reversed above this threshold. The variation in abundance of these two groups of Cladocera could thus be the result of a passive competition, in which the development characteristics in relation to temperature play the major role.

No interpretation of the seasonal variation in abundance of the Calanoids in zone 2 is satisfactory. Temperature cannot be the cause as this does not explain the disappearance of this group during the rainy season. *Tropodiaptomus* has a high optimum temperature (24.1°C) and it appears, from other characteristics of the relationship of the duration of embryonic development to temperature, to be one of the species least sensitive to thermal factors. A general explanation can be put forward, according to which *Tropodiaptomus* is a pelagic form, thus well adapted to the north basin, deeper and not affected by the flood. In the south basin, the low temperatures occurring during the cold season and/or the low level of the lake at the period of low water, accompanied by a slight increase in turbidity could have provoked, by unknown factors, the reduction of this group during the cold season and between June and September. This would appear to be more plausible for this species, which progressively disappeared in 1973 with the lowering of the water level. Other intervening factors combining with each other or with the preceding factor may have been: variation in algal biomass, variation in the production rate and in predation pressure (Fig. 7). The decrease in phytoplankton biomass, production rate (or birth rate), and the high zooplanktophagous fish stock, would thus contribute to

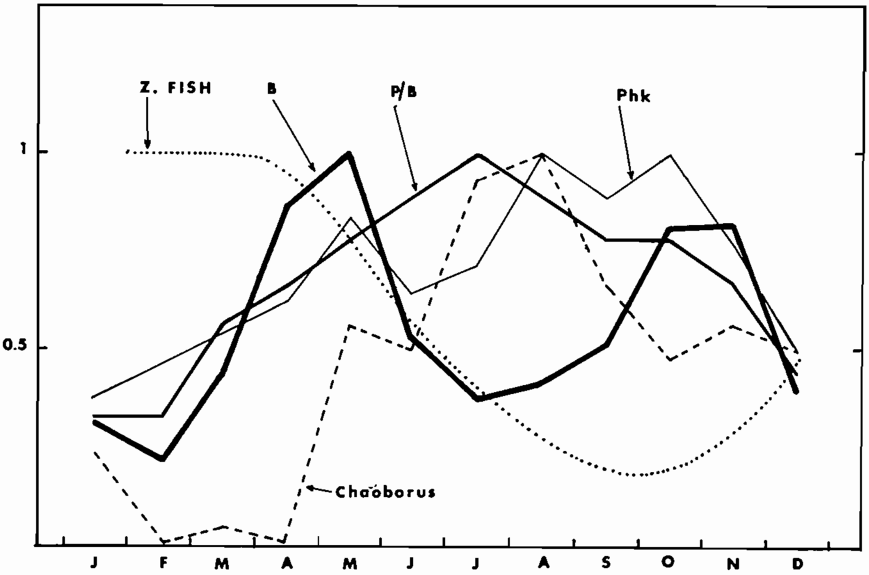

Fig. 7 Seasonal variations in the abundance of zooplanktophagous fish (z. fish), of *Chaoborus* larvae, of phytoplankton (Phk), of production rate (P/B) and biomass (B) of Diaptomids over an hypothetical annual cycle in the southern archipelago during the period of 'Normal Chad'. Every monthly value has been divided by the corresponding annual maximum.

the decrease in Calanoids in the cold season, but the reasons for the decrease between June and September are not clear.

More generally we must emphasize that a decrease in abundance occurred approximately between June and September throughout the south basin, and affected all the species, with the possible exception of *C. cornuta* (Fig. 3). At station II (zone 1) we saw that it was probably started by an increase in turbidity, due to intensive resuspension of bottom sediments by the waves, then maintained by some other factors in particular the reduction in algal density. This explanation would not appear to be valid in zone 2, because there was no decrease in transparency or algal density (Fig. 8), and no increase in turbidity was noticeable at this time. The only possible factor appeared at first to be an increase in the numbers of *Chaoborus* lsrvae (Fig. 7). However it would seem unlikely that this increase was sufficient to cause a considerable and rapid decrease in zooplankton, so that this major aspect of the seasonal variations in the zooplankton populations observed over all the south basin, has no satisfactory explanation.

In conclusion, no single factor appeared to govern the level of zooplankton abundance in Lake Chad or to regulate its regional or seasonal variations, which remained low. Among the factors cited, the temperature, which was

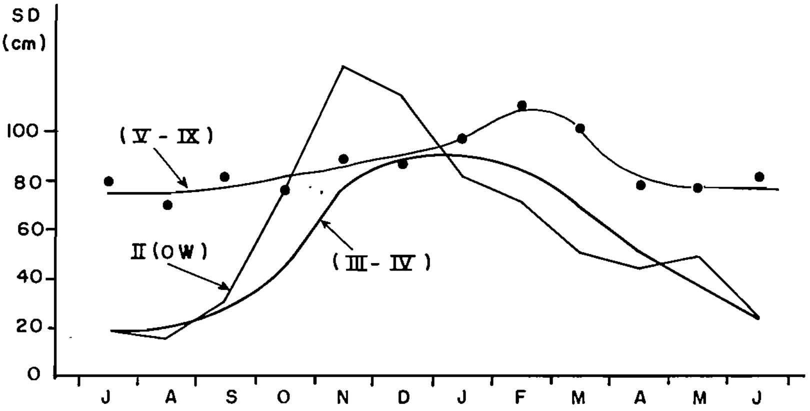

Fig. 8 Secchi disc transparency at station II (open waters), III–IV (reed islands) and V–IX (archipelago) in 1964–65 in the south basin (after Gras et al. 1967).

identical in all the biotopes considered, was only responsible for small quantitative variations affecting the Cladocera. On the contrary the most important factors seemed to be the Shari flood in the south basin and the greater depth in the north basin, as they were directly responsible for the lowest densities observed in the two regions.

7.2 Community changes during the establishment of 'Lesser Chad' (1972–1975)

7.2.1 *Structure and composition of the zooplankton community*

In spite of a progressive lowering of water level, it is reasonable to state that the zooplankton population changed little until 1971, or even 1972. After this period profound modifications occurred, that were well studied in the archipelago of the south basin.

7.2.1.1 *Changes in the populations in the archipelago of the southern basin.* Until 1972, the lake could be considered to be in a state of 'Normal Chad' from the point of view of water area, and there was a communication between the water masses inside the archipelago and the open water. After December, the water area decreased rapidly, with the emergence during April–May 1973 of all the regions of the reed islands. The open waters of the archipelago were isolated and then progressively reduced to several ponds fairly large and deep, most of which dried up before a partial recovery of the water occurred in October. The changes in the community were successively followed at 3 stations in the archipelago, Tchongolérom, Lafia and Bol (Fig. 1), but not until a final drying up stage.

Because of the agreement in the structures observed at these stations (Table 2) it is possible to describe the changes in comparison with 'Normal Chad.' The populations of 1972 (May to October) differed essentially in: (a) the low densities of *Bosmina*; (b) the return of large numbers of *Thermodiaptomus*; (c) the presence of a considerable number of littoral Cladocera (genera *Alona* and (*Macrothrix*). In 1973 changes were rapid and one observed: (a) the quasi disappearance of Cladocera other than *Moina* and *Diaphanosoma*; (b) the disappearance of *Tropodiaptomus* and its replacement by *Thermodiaptomus* which also decreased during April–May; (c) the development of cyclopoids, particularly *Th. neglectus* and the disappearance of *Th. incisus circusi*, not very abundant during the period of 'Normal Chad'.

In addition to the modifications in species composition, a change in the demographic structure of all the populations was observed characterized by an increase in the proportion of adults, by weight. Littoral forms remained numerous and a great increase in Rotifer numbers was observed, evaluated only in three samples. Thus, 3836 rotifers per liter were counted, and 467 microcrustacea per liter, of which 82% were nauplii, on 9/4/73, at Tchongoleron. Similar values were obtained on 1st/2nd. May at Lafia, with rotifer counts of 2974 l^{-1} and 2436 l^{-1}, and microcrustacean counts of 1151 l^{-1} and 1216 l^{-1} (92% and 83% nauplii). Rotifer numbers in May 1965 were only 47 l^{-1} in the archipelago, rising to 111 l^{-1} in February 1971. This change, which eliminated or masked the seasonal variations of 'Normal Chad', occurred, without major changes in total population density until May 1973, even July, when the qualitative observations made at Bol-Berim in a study on embryonic and juvenile development showed that, at that time, the population again had the same characteristics as in May. The considerable fall in biomass during August may have been caused by similar reasons to those that caused sporadic mortality of fishes at much the same time in the same region (Chapter 10).

After the return of water in October, the community showed some characteristics in agreement with the development shown above, with essentially, 3 species, *Moina*, *Diaphanosoma* and *Th. neglectus* (Table 3). Only *Thermodiaptomus* did not reappear and the zooplankton did not include any Calanoids. Three other important features were noted: (a) the densities were very low, with 56.4 mg m^{-3} on average for the non-zero values of 1974–75 and an absolute maximum of 142 mg m^{-3}; (b) *Mesocyclops*, a carnivorous species in 'Normal Chad', disappeared after the low water period of 1974; (c) the abundance of littoral forms was not as great as might have been expected with the considerable development of vegetation.

It is interesting to note that the two Cladoceran species subsisting at the end of this period were, at their maximum density, with some variation, similar to their densities in the high water period: 26.7 mg in February and April 1973; 38.3 mg in the same months in 1965 and 30.4 mg in February 1971. The void left by the Cladocera was thus not filled by species of the same group, but rather

Table 3 Densities of planktonic crustacea (mg dry weight m^{-3}) and some littoral forms of Cladocera (N m^{-3}) at Bol-Berim in 1973, 1974 and 1975. In total, for all the samples taken, representing 12.497 m^3 filtered water, one C_5 and one female of *Thermodiaptomus* were observed.

Dates	Crustacea								
	Moina	*Diaphanosoma*	*Ceriodaphnia*	*Bosmina*	*Thermocyclops neglectus*	*Mesocyclops leuckarti*	Total	Cladocera (total %)	Littoral forms (N m^{-3})
12/08/73	0.1	0.1	0	0	3.6	ε	3.9		107
7/11	0.4	ε	0	ε	0.1	ε	0.7		1253
12/12	0.1	0.4	ε	0	0.8	0.2	1.5		699
17/01/74	0.1	ε	0.3	ε	10.9	0.3	11.7	4.1	1605
2/03	0.4	0.1	0.2	0	7.0	0.2	7.9	9.7	81
18/04	41.1	0.1	0	0	26.9	3.0	71.2	57.9	137
16/05	17.9	18.6	0	0	38.9	ε	75.4	48.4	136
22/07	5.9	15.5	0	0	45.6	0	67.0	32.0	2877
15/09	8.2	6.5	0	0	18.5	0	33.2	44.1	491
21/10	0	0	0	0	0	0	0		0
11/12	ε	0	0	0	0	0	ε		0
23/05/75	16.4	36.0	0.2	0	89.8	0	142.4	36.9	0
2/09	13.5	10.7	1.1	0	17.2	ε	42.4	59.5	310
1/12	ε	ε	0	0	ε	0	ε		0

by *Th. neglectus*. The only change which occurred after October 1974 was the disappearance of *Mesocyclops* which was presumed to have kept to the carnivorous diet shown previously. Its disappearance was probably caused by the five-fold decrease in the microcrustaceans, especially Cladocerans, upon which it normally fed, particularly if one takes into consideration the almost certain frequent occurrence of cannibalism by the adults and later carnivorous stages upon the earlier stages.

The profile of variations in abundance after October 1973 (Fig. 9) can be compared with that of the peri-deltaic zone (station I, Fig. 3a), which had some zero values. It differed by having a very late and much slower increase in biomass, which, as already indicated, remained very low. The water entering the archipelago after October were filtered by the abundant vegetation which had become established between the open water and the archipelago; these waters lacked zooplankton, were very poor in oxygen, and contained dissolved CO_2 (Benech et al. 1975). These unfavourable conditions continued until almost February, and undoubtedly were a partial explanation of the slow development of the zooplankton in the cold season. Events occurred as if the development of phytoplankton and zooplankton were independent of one another (Fig. 9).

It will be noted that *Moina* and *Diaphanosoma* developed less rapidly than *Th. neglectus*, whose development cycle must nevertheless be much longer. It has to be compared to the fact that in the period of 'Normal Chad' the two Cladodera were summer forms whereas *Th. neglectus* was, among the Cyclopoids, relatively well developed in the cold season.

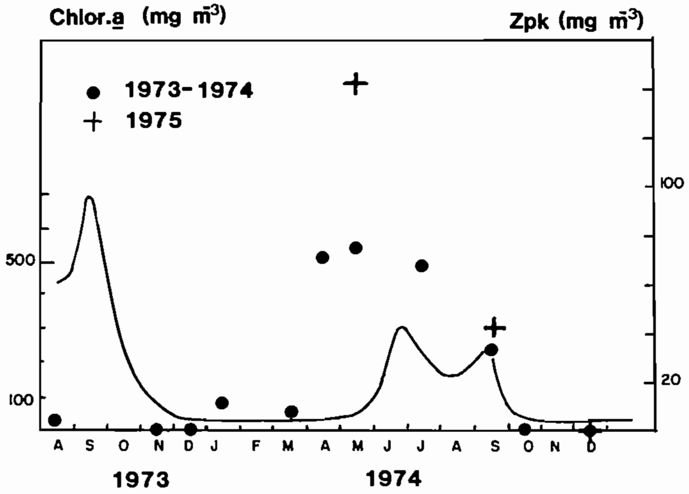

Fig. 9 Variation in chlorophyll concentration (plain line) and in zooplankton density (circles and crosses) at Bol-Berim in 1973–74.

None of the following factors — a change in salinity or in water composition (which were not so different in 1974–75 from those of 'Normal Chad'), insufficient food, or an over-abundance of zooplanktivorous species — appear to be the cause of low densities in 1974–75. The chlorophyll concentrations were indeed identical or even higher than those of 'Normal Chad', and the zooplanktivorous *Brachysynodontis batensoda*, still abundant, tended to change from a strict zooplanktonic diet in the high water period to a diet of detritus. Moreover, there was a growth check in 1973 and in 1974, the year during which the fish disappeared (Benech 1975; Im 1977). However a change in phytoplankton composition was noted. Euglenoids becoming dominant. These changes may have been important, but the most probable cause of low density levels was a permanent deficit of oxygen. Although oxygen tensions of 75–100% saturation were still noted in the whole water column during 'Normal Chad', they were much lower in 1974–75, being 5 to 60% saturation at the surface, with intermittent creation of almost anoxic conditions in the deeper layers of the entire water column (Chapter 10). This situation could have caused raised natural mortality rates, slowing down of reproduction, accumulation of organisms in the upper layers, or the three phenomena together.

7.2.1.2 *Changes in the other regions. The open water of the south basin.* Available data from the station nearer to the delta than station II in 1964–65 (Table 4) showed that as no profound changes in environmental conditions occurred in this region, the populations retained the same characteristics as those of 'Normal Chad'. This made it difficult to interpret the differences observed in 1973–74. One can however consider the densities in 1973–74 to be comparable with those obtained for the corresponding months in 1964–65, 1969 and 1971, although systematically lower. The zooplankton was moreover fairly well diversified with seven relatively abundant species, including *Tropodiaptomus incognitus.*

The north basin. A single series of data is available for this region from October 1973 a time, when the changes had ended in the south. These data refer to the east central part of the north basin in which 14 stations were sampled. They were situated in the three main types of natural zones already distinguished: open water, reed islands, and archipelago. The community was almost as diverse as during 'Normal Chad', with nine species, including *Tropodiaptomus*. Although the scarcity of *Bosmina longirostris* must be noted, it can't be attributed with some precise significance to the quasi disappearance of this species. The average population density (483 mg m^{-3}) was higher compared with the data of February 1971 (about 200 mg m^{-3}, cf. Table 1), but this corresponded to the seasonal maxima noted in zone 3 during 'Normal Chad' (514 mg m^{-3} in April 1965 and 440 mg m^{-3} in November 1964). The coefficient of variation of the mean population density were also greater than in 1971: 57% compared with 43% in 1971.

Table 4 Densities (in mg dry weight per m^3) observed in the center part, east of the north basin, and in the open water of the south after the drying of the southern archipelago, Copepod nauplii excluded.

Zones	Dates	Z	Densities (mg m^{-3})									
		(m)	M.m.	D.e.	C.c.	D.b.	B.l.	T.n.	M.l.	T.ic.	T.i.	Total
Open water		1.40	28.7	56.2	0.3	120.8	4.0	4.7	47.5	4.7	325.0	591.9
		1.44	62.9	102.5	0.9	92.5	2.7	6.2	42.0	11.4	187.8	508.9
		2.00	5.5	10.5	0.1	35.8	1.1	1.0	4.2	2.3	53.3	113.8
		2.18	22.3	33.2	1.5	30.4	0.1	2.7	11.5	3.0	125.8	230.5
Archipelago	18–25/	0.95	252.6	73.7	16.0	70.1	0.7	10.0	33.0	9.0	206.0	671.1
and Reed		1.37	63.5	111.0	9.4	144.1	2.1	7.3	22.2	15.4	314.5	689.5
Islands	10/73	2.21	100.3	38.6	17.3	94.0	0.4	3.9	13.6	7.5	226.0	501.6
		1.93	46.1	53.1	11.0	72.7	1.0	3.0	22.3	7.9	265.4	482.5
		2.49	31.5	20.1	11.6	23.6	0.1	3.6	10.4	3.5	106.2	210.6
		2.06	18.8	12.2	6.1	12.1	0.1	3.3	21.5	3.2	114.8	192.1
		1.08	141.4	39.1	55.1	258.8	0.1	11.8	18.6	6.5	189.2	720.6
		0.97	309.2	43.3	87.8	309.2	0.3	16.4	31.5	7.8	268.3	1073.8
		0.82	221.5	36.0	33.8	200.9	1.7	17.0	23.1	2.2	167.5	703.7
		2.74	6.6	2.0	0.3	10.6	2.4	15.2	6.2	0.1	24.6	68.0
South Basin	18/04/73	1.72	42.6	18.0	0.3	0	0.5	136.4	7.0	0.3	14.6	219.7
Open Water	12/01/74	1.72	11.0	2.8	3.1	0.7	10.5	42.2	1.4	E	20.8	92.5
	4/02/74	1.74	14.8	7.3	1.6	0	9.6	46.4	0.9	0	15.4	96.0
	13/03/74	1.55	31.3	21.7	0.2	0	2.3	37.7	0.4	0	2.3	95.9
	6/10/74	2.61	11.9	42.7	3.5	0	2.9	12.8	3.5	0	5.0	82.3
	2/12/74	2.12	3.4	0.9	1.3	0	5.8	9.1	0.3	0	14.0	34.8

The population of this region which was similar to the normal stage changed with the lowering of the water level. It is possible that, in view of what happened to the phytoplankton, these changes did not exhibit the same features as in the southern archipelago, if one considers maximum levels of conductivity: 1120 and 3530 μS cm^{-1} respectively for the 1974 min. and max. values, while the 1973 maximum in the southern archipelago was 524 μS cm^{-1}.

7.2.2 *Annual variations in density and stock (1964–73)*

The zooplankton density remained almost constant at about 300 mg m^{-3} from 1964 to May 1973 in the southern archipelago (Fig. 10a, Table 2). This relative

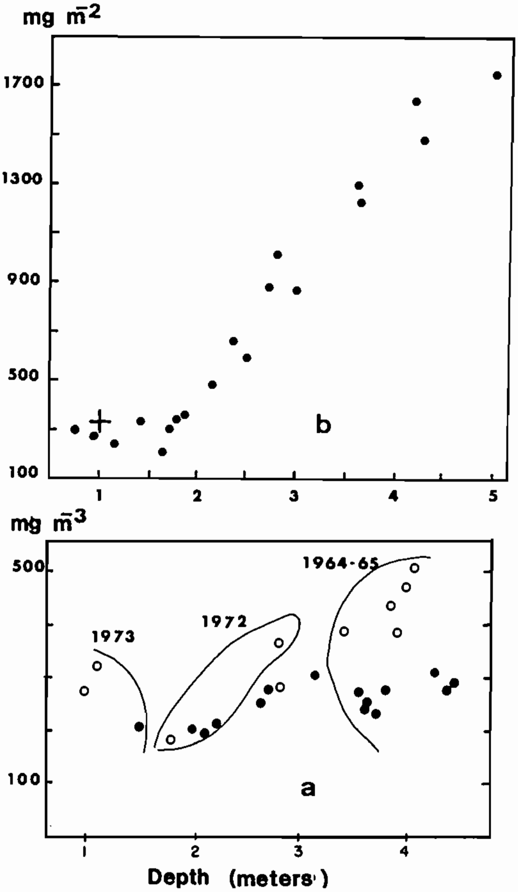

Fig. 10 Yearly variation of density and biomass per m^2 in the southern archipelago from 1964 to 1973. In (a) the plain circles represent the seasonal minimums.

constancy persisted in spite of the changes already described in structure and composition of the population in which the Copepods remained dominant (63% of the biomass in 1964–65, 87% and 90% in January and April 1973). However, two facts indicate a slight lowering of densities, which may have begun in 1972 with the quasi disappearance of the genera *Bosmina* and *Daphnia*. The higher densities observed in 1964–65 were never reached in following years, and the seasonal minima of the period 1972–73 were lower than the threshold of 240 mg m^{-3} above which all the values found during the period of 'Normal Chad' were situated.

The density remained about the same, the biomass per unit area decreased almost proportionally to the lowering of the water level (Fig. 10b), and the stock decreased in proportion to the decrease in volumes. This stock was distributed very unevenly between the three zones distinguished at the 'Normal Chad' stage, following the unequal distribution of water volume. In February 1971, for a water level height of about 281.30 m, the north basin thus contained 60% of the lake zooplankton stock estimated at 12 200 tons (Fig. 11). The biomass per hectare was evidently much higher in the north. If one extrapolates to the water level of 283 m, which was present in 1964–65, keeping the same densities and the same areas under water, one observes a small change in the stock distribution (55% in the north) and significant changes in the biomass per hectare (12.5 kg in zone 3, 12 kg in zone 2 and 4.2 kg in zone 1). These changes were the result of a relatively greater increase in depth (1.70 m) in the south than in the north.

At Bol station, which is supposed to be representative of the archipelago, the gross phytoplankton production ($mgO_2m^{-2}\ h^{-1}$) remained almost constant from 1968 to 1975 with some increases during the last year (Chapter 11). The chlorophyll concentrations or phytoplankton densities also markedly increased (Fig. 12). The decrease in grazing (lowering of the stock of zooplankton) would have contributed to this increase, without being the major cause (Chapter 12). Be that as it may, these data tend to show that zooplankton abundance was not proportional to that of phytoplankton. They support the fact that no clear dependence was found between the two biocoenoses, as seen in 1973–74 (although conditions differed, Fig. 9) or when comparing the annual cycles of 1964–65 for the zooplankton (Fig. 3) and 1969 for the phytoplankton (Fig. 7). In the first case, the curve is clearly bimodal, and it is almost unimodal in the second.

Thus, it appears that the phytoplankton biomass and its production were not the factors limiting the zooplankton, in any of the periods of change in the lake. This may not have been so during certain periods in zone 1 where algal densities were very low and the ratios of phytoplankton and zooplankton abundance were much lower than in the archipelago (Fig. 13). However, if one decides that phytoplankton was not limiting, variations in zooplankton abundance and diversity must have been regulated primarily by the presence of several

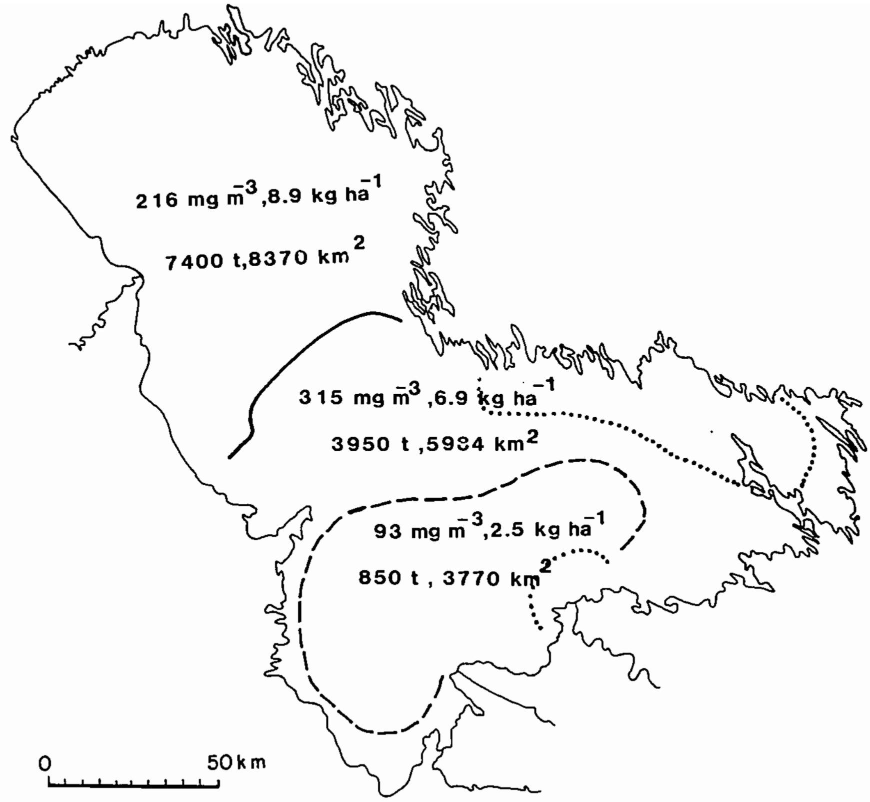

Fig. 11 Stock and biomass per hectare in zone 1, 2 and 3 in February 1971, calculated for a of water level altitude 281.30 m.

zooplanktophagous species, or more generally by the essential importance of the pelagic food chain in 'Normal Chad'. Simplified examples of such regulation are offered by Lago di Anone (Bernardini and Giussani 1978). After the disappearance of the zooplanktivorous *Alburnus alburnus alborella* from a part of the lake, it results in strong oscillations in the *Daphnia hyalina* population, which was previously very stable. In such conditions, supposing that food is always in excess in the southern archipelago of the lake, the annual stability of density is explainable, in spite of the changes in structure or composition of the phytoplankton, the zooplankton and the zooplanktivorous species. Some experimental observations (Hall et al. 1970) suggest that an increase (or a decrease) in the predation pressure has no influence on the mean zooplankton abundance, but only on its composition or diversity, provided that the nutritional conditions are favorable (which was the case in enriched ponds studied by the authors). Other data appear to confirm the absence of a direct or close relationship between the

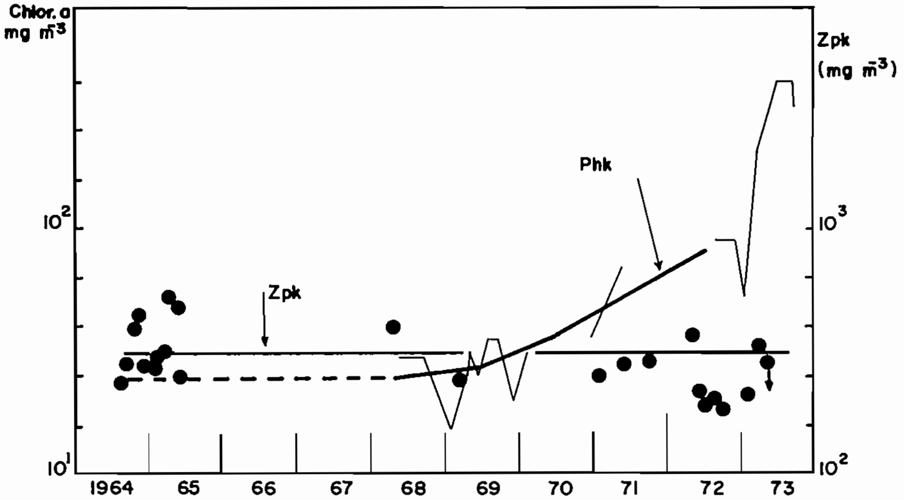

Fig. 12 Changes in chlorophyll concentration and zooplankton density, for the high water period until the drying up, in the southern archipelago. For the phytoplankton, the thick line shows an adjustment by eye of the data of Lemoalle (1973) representing the yearly evolution. The fine lines correspond to the short period variations corresponding to the measurements. For the zooplankton, the horizontal lines shows the general mean of annual values obtained.

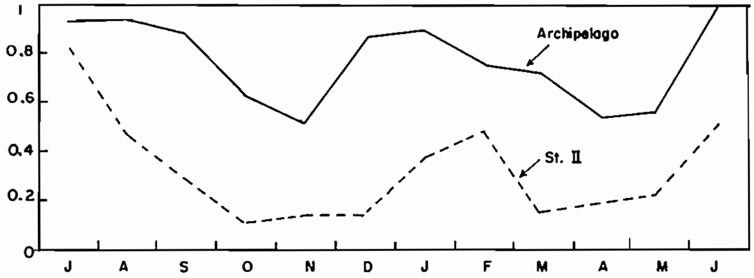

Fig. 13 Ratio between the numbers of cellular algae per liter and the zooplankton biomass (mg m^{-3}) in the southern archipelago and station II in 1964–65 (relative values, expressed by comparison to maximum archipelago value of June 1965: N/B value month X divided by N/B value in June).

phyto- and zooplankton biomasses, when the former exceeds a certain threshold. Apart from Lake Chad, where the zooplankton density was almost the same both in the high water period and in 1973 with very different chlorophyll concentrations (20 to 40 mg m^{-3} in 1968–69; 60 to 280 mg m^{-3} from January to April 1973), one can quote Lake George (370 mg m^{-3} zooplankton for 177 mg m^{-3} chlorophyll); Loch Leven (350 mg m^{-3} average for 10 to 250 mg m^{-3}

chlorophyll) Lake Naivasha (202 mg m^{-3} for 20 to 50 mg m^{-3} chlorophyll), and two more eutrophic reservoirs (thus having *a priori* a high chlorophyll concentration) from South Africa, Lakes Hartbeespoort and Rietvlei, (about 400 mg m^{-3} zooplankton, Seaman 1979). Among the data considered here, low chlorophyll concentrations occur with low zooplankton: Lake Ototoa has a mean of 1 mg m^{-3} chlorophyll (from 0.04 to 4.6 mg m^{-3}) for 12 mg zooplankton, and two oligotrophic lakes of South Africa (Lake Lindleyspoort and Buffelspoort) studied with the two previous eutrophic lakes, support zooplankton densities of 30 and 50 mg^{-3}. These data are insufficient and too heterogeneous to predict whether or not a relationship exists between the mean zoo- and phytoplankton concentrations, and in particular if, as suggested by some previous data, there is a fixed limit for the high concentrations, by supposing that chlorophyll is a good indicator of phytoplankton abundance. In the range of the high concentrations, the variations in phytoplankton abundance would have been reciprocated by some changes in the structure or the production rate of the zooplankton population such as seen in Lake Chad (Chapter 12). In all hypotheses, it will be noted that the annual changes in zoo- and phytoplankton abundance express a total decrease in ecosystem efficiency which leads to the end of the preponderance of the pelagic transfer chain. From this point of view, the situation in the southern archipelago in 1973, is more similar to Lake George than to 'Normal Chad'.

7.3 General characteristics of the community

7.3.1 *Species richness*

Compared with some well-studied African lakes (Table 5), the Lake Chad community in the high water period would seem to be one of the most diverse in Africa, with 9 abundant species, of which seven (3 Cladocera, 1 Calanoid and 3 Cyclopoids) were simultaneously present and abundant throughout the year. Comparison with some other biotopes sampled occasionally, sometimes for faunal inventories, leads to the same conclusion. Among the large East-African lakes, the zooplankton of Lake Tanganyika in the pelagic zone consists of 3 Copepods (*Diaptomus simplex*, *M. leuckarti*, *Th. schurmanni*) (Lindberg 1951) and that of Lake Kivu, 3 Cladocera and 3 Cyclopoids, based on the data of Lindberg (1951) and Harding (1957). Collections in smaller water bodies have also been made. Jebel Aulia (Monakov 1969) with 11 species of which 3 are Copepods, is relatively diverse, and 4 small lakes of the Cameroon contained monospecific populations at the time of sampling, with either *M. leuckarti* (Lake Soden) or *Thermocyclops hyalinus* (Lake Mborombi Mbo, Kotto, Mboandong) present (Green 1972). Without attempting an exhaustive inventory, which is after all very difficult, it appears that the situations are all too diverse under other latitudes and emphasize the diversity of Lake Chad community (Weglenska 1971; Comita 1972; George and Edwards 1974; Kwik and Carter 1975; Salanki and Ponyi 1975; Rey and Capblancq 1975; Green 1976; Lair 1977, 1978; Gophen 1978). In Lake Lipno (temperate cold) (Brandl 1973), the population consists of eight species of which 5 are Cladocera. On the other hand the crustacean zooplankton communities of Loch Leven (cold temperate) or of Lake Kinneret (14–28 °C) are almost monospecific, with *Cyclops strenuus abyssorum* and *M. leuckarti* respectively (Burgis and Walker 1972: Gophen 1978).

The diversity of the Lake Chad populations may be due to the large size of the lake, to the diversity as well as the abundance of food (about 25 mg m^{-3} of chlorophyll *a* in 1968–69 at Bol, or 1400 mg wet weight of phytoplankton per m^{-3} in the whole southern archipelago in 1971), and to the permanence of favourable temperature conditions. The strong thermal gradient (18–30°C) and the existence of relatively low temperatures over a fairly long period of the year were the causes of diversity, because they allowed the cold water forms *Bosmina* and *Daphnia* to establish themselves, as well as others which were well adapted to the thermal conditions of the environment. In Table 5, one notes that *B. longirostris* is present and the genus *Daphnia* is diverse in Lake Chad, Lake Midmar (South Africa) and Lake McIlwaine (Zimbabwe) which have the lowest minimum temperatures. The fact that the predators contribute to increased diversity and stability of the plankton community has been shown in some cases (Hall et al., 1970; Dodson 1970; Lane 1978; Zaret 1978). The existence in the lake of a large number of vertebrate and invertebrate predators is also favourable to species richness. In the archipelago, the zooplanktivorous fishes were numerous and represented a high fraction of the ichthyomass, about 44% according to calculations made from 1966 to 1970 (Lauzanne 1972). Two of these fish, *Alestes baremoze* and *Brachysynodontis batensoda* (27% of total ichthyomass) are respectively macro- and microphagous complementary predators. To these predators must be added other fish, *Chaoborus* larvae, 2 Cyclopoids, and the juveniles of several fish species. This situation can be contrasted with that of Lake George, where the zooplankton is less diverse and the zooplanktivorous species less numerous consisting of *Chaoborus larvae*, *M. leuckarti* and one fish of secondary importance, *Haplochromis poppenheimi* (Burgis et al. 1973).

The decrease in the number of species which began in about 1972 in the archipelago, was accompanied by a reduction in the number of zooplanktivorous species since *B. batensoda* alone existed to the end of the community changes, this species having mainly a detritivorous diet. It is thus possible that there was a cause and effect relationship between these two phenomena, but the hypothesis that the disappearance or scarcity of certain zooplankton species is due to a change in environmental conditions is quite valid. These two factors are not exclusive of each other as the Cladocera that

Table 5 Characteristics and composition of communities of planktonic microcrustacea from some well-sampled African lakes; * = abundant or dominant species, by numbers or by weight; A = artificial; N = natural; E = eutrophic; O = Oligotrophic or mesotrophic.

Lakes	Type	Latitude	Altitude (m)	Area (km²)	Mean depth (m)	Surface Temp. (°C)	Species	References
Chad	N E	12°30 N	282	18 000	3.9	18–30°C	*Diaphanosoma excisum**, *Daphnia barbata**, *D. longispina*, *D. lumholtzi*, *Ceriodaphnia affinis*, *C. cornuta**, *Moina micrura**, *Bosmina longirostris**, *Tropodiaptomus incognitus**, *Thermodiaptomus galebi*, *Thermocyclops neglectus**, *Th. incisus circusi**, *Th. tchadensis*, *Mesocyclops* cf. *leuckarti**	present work (high water)
George (Uganda)	N E	0°	913	250	2.25	25–26	*Thermocyclops hyalinus***, *Mesocyclops* cf. *leuckarti**, *M. micrura*, *C. cornuta*, *D. barbata*	Burgis (1974)
Chilwa (Malawi)	N	15°15 S	654	700	2	21–28	*D. excisum**, *D. barbata*, *M. micrura*, *C. cornuta*, *Tropodiaptomus kraepelini**, *M.* cf. *leuckarti**	Kalk (high water)
Naivasha (Kenya)	N E	0°46 S	1890	145	4.7	19.5–23	*D. excisum**, *Simocephalus vetulus**, *Thermocyclops** *schurmanni*, *M. cf. leuckarti**	Litterick et al. (1979)
Mc. Ilwaine (Zimbabwe)	A		1370	26.3	9.5	16–28	*D. excisum*, *Daphnia laevis*, *D. lumholtzi*, *Ceriodaphnia dubia***, *M. dubia*, *B. longirostris*, *Tropodiaptomus orientalis*,	Munro (1966)

							Tropocyclops prasinus, *Thermocyclops emini*	
Midmar (South Africa)	A O	29°S	1000	15.6	11.4	11–25	*D. excisum*, Daphnia pulex*, D. longispina*, D. tenuispina, D. barbata, M. micrura, B. longirostris, Tropodiaptomus spectabilis*, Metadiaptomus transvaalensis, Thermocyclops oblongatus, Th. tchadensis, Thermocyclops retrocurvus*	Akhurst et al. (1979)
Turkana (Kenya)	N	2–4° N	406	7200	~80 max.		*D. excisum*, D. barbata, C. cornuta, Moina brachiata, Tropodiaptomus banforanus*, M. leuckarti*, Th. hyalinus**	Ferguson (1974)

Table 6 Zooplankton abundance in some African and temperate lakes (* corresponds to less accurate data, generally through graphical estimates).

Lakes	Depth (m)	Surface temp. (°C)	Mean density		Maximum density	Maximum/ minimum	$g\ m^{-2}$	Remarks	References
			dry weight $mg\ m^{-3}$	$Nb\ l^{-1}$					
Chad (Archipelago)	3.9	18–30°C	333	318	515 mg 453 indiv.	2.2	1.3	annual mean (a.m.)	present work
Chad (Zone 1)			181	152	413 mg	6.3		a.m.	present work
George	2.25	25–26	368		600 mg	1.8	0.8	a.m.	Burgis (1974)
Chilwa		21–28			100–800 ind.	~50 à 400		high water, limited data	Kalk (1975)
Naivasha	4.7	19.5–23	202*		364* mg	4.9	1.0	a.m.; $DW/m^2 = DW/m^3 \times 4.7$ m.	Litterick et al. (1979)
Turkana	80 max.			200*		3.5*			Ferguson (1975)
Loch Leven	3.9	0–19	350*		1030* mg	30*	1.37*	a.m. *Cyclops strenuus abyssorom*	Burgis and Walker (1972)
Eglwys Nynydd	3.5	0–18	445	50*	2030 mg	50*	1.6	a.m., 1970 and 1971; values related to *Daphnia hyalina* (dominant species in the community)	George and Edwards (1974)
Lipno	6.6	~18	160	—	—	—	1.25	May–October mean (30 values for several stations from 1960 to 1967); mg DW = mg N × 8.33	Brandl (1973)
Mikolajskie	11.7	~16	933	—	—	—	—	Summer mean (22/07–30/08/64) mg DW = 0.10 mg FW	Weglenska (1971)
Balaton			100 70	—	—	—	—	May–November 1965, 66 and 67; values for 2 regions of the lake:	Salanki and Ponyi (1975)
Ototoa	12–16[a]	10–25	11.7		14.2 mg	1.7	0.21	*Calamoecia lucasi* only (75% total number);	Green (1976)
Kinnereth		14–28	—	—	—	2.7*	1.5*	a.m.; *M. leuckarti*	Gophen (1978)

[a] Metalimnion depth.

disappeared were the winter forms, of which two, *D. longispina* and *B. longirostris*, are cosmopolitan or widespread in temperate regions. These species must be at the limit of favourable thermal conditions in Lake Chad and they continued to develop as other environmental aspects (abundant food, considerable predation pressure, existence of appropriate conditions in a true pelagic zone), allowed them to compete with the other very ubiquitous species, which were well adapted to the thermal regime of the lake. Thus it is not surprising that these forms have not survived the rapid transformation of environmental conditions during the establishment of the 'Lesser Chad'.

If the size criteria of Dodson et al. (1976) are adopted the lake community could be placed in the category of small zooplankters (0.2–0.3 mm length) which are generally subjected to strong predation pressure.

7.3.2 *Abundance*

The mean biomass and the annual variations observed in the actual lacustrine part of Lake Chad (zones 2 and 3) were of the same order of magnitude as those of Lakes George, Naivasha, and Turkana which are among the best known African lakes (Table 6). Although other more partial data are similar, there are also data which differ. Monakov (1969) mentions 300 mg m^{-3} (April) and 150 mg m^{-3} (autumn) for Jebel Aulia; Seaman (1979) from 30 to 400 mg m^{-3} annual average for small reservoirs in South Africa, according to their trophic state: 30 and 50 mg m^{-3} for two oligo- and mesotrophic lakes and 400 mg m^{-3} for two eutrophic lakes. One can also include the values reported by Green (1972) for 4 smaller Cameroon lakes (from 2 to 53×10^3 individuals m^{-3} in April), and by Rufli (1976) for Lake Tanganyika (1890 ind. m^{-3} in May 1976), these numbers being low when compared with those of Lake Turkana or Lake Chad.

The insufficient number and the heterogeneous or incomplete character of data collected up to now on the African biotopes as well as from other continents or climatic zones; show that a valid comparison of average densities may not be made. The few data shown in Table 6 do not show any major differences between temperate and tropical environments from this point of view.

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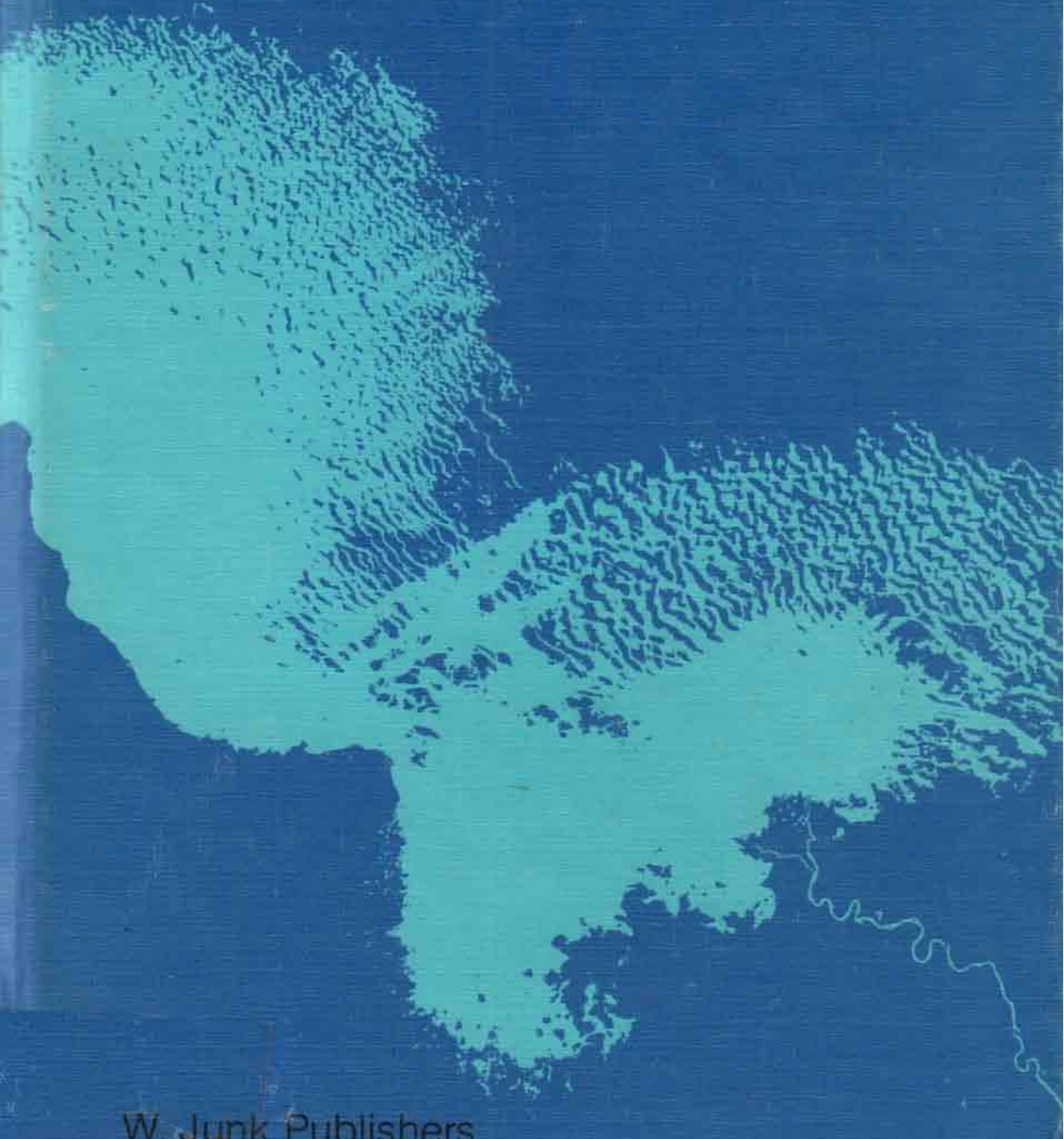

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Ecology and Productivity of a Shallow Tropical Ecosystem

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1983 **Dr W. JUNK PUBLISHERS**
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THE HAGUE / BOSTON / LANCASTER

Distributors

for the United States and Canada: Kluwer Boston, Inc., 190 Old Derby Street, Hingham, MA 02043, USA
for all other countries: Kluwer Academic Publishers Group, Distribution Center, P.O.Box 322, 3300 AH Dordrecht, The Netherlands

Library of Congress Cataloging in Publication Data

Main entry under title:

Lake Chad.

(Monographiae biologicae ; v. 53)
Includes bibliographies and index.
1. Lake ecology--Chad, Lake. 2. Biological
productivity--Chad, Lake. 3. Chad, Lake. I. Carmouze,
Jean-Pierre. II. Durand, Jean René. III. Lévêque, C.
IV. Series.
QP1.P37 vol.53 574s [574.5'26322'096743] 83-4288
[QH195.C46]
ISBN 90-6193-106-1

ISBN 90-6193-106-1 (this volume)

Cover design: Max Velthuijs

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PRINTED IN THE NETHERLANDS